Intraspecific competition and spatial heterogeneity alter life history traits in an individual-based model of grasshoppers☆

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Abstract

An individual-based model (IBM) was developed to examine the effects of intraspecific competition and spatial structuring of food on life history traits of grasshoppers inhabiting temperate-zone grasslands. Each individual carried real-valued genes which determined size of offspring and size at maturity, and which were passed on to its offspring. Size at maturity was a plastic trait, depending on an individual's growth rate, whereas size of offspring was a fixed trait. Individuals with more successful combinations of traits produced more offspring that eventually came to dominate the population. Populations were food limited and intraspecific competition was either exploitative or size-based interference. Growth rates and fecundity depended on food quality, which declined within season as a function of day of year and the proportion consumed by grasshoppers. Three different spatial distributions of food quality were examined: uniform, random, and clumped. Optimal egg size was larger under interference competition and spatially clumped resources. Reaction norms of size at maturity were strongly affected by type of competition, and, by spatial distribution of resources within exploitative competition, but not under interference competition. The IBM shows promise as a means of analyzing life history evolution in grasshoppers in relation to processes that arise from localized interactions between individuals.
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1. Introduction

Several species of grasshopper (Orthoptera: Acrididae) cause sporadic, but sometimes severe, economic losses to crops and rangeland in many parts of the world. Because of their prominent status as economically important pests, certain species of grasshoppers have been the subject of numerous studies, from the molecular to ecosystem level (Chapman and Joern, 1990; Gangwere et al., 1997). One aspect of their biology that has not received a great deal of attention concerns the evolution of life history traits. A better understanding of the forces shaping life history attributes of grasshoppers would lead to better predictions of subsequent population dynamics under changing environmental conditions (Joern and Gaines, 1990; Nylin, 2001). This paper describes an individual-based model (IBM) of the ecology and life histories of grasshoppers of North American grasslands. The model is used to explore how intraspecific competition and spatial patterns of resource

availability affect selection pressures on key life history traits.

1.1. General description of grasshopper biology and ecology

Acridids in temperate regions exhibit many different variations on a common life history theme. In northern areas, generations are non-overlapping, but in more southern areas where more than one generation per year is possible, there may be partial overlap. Typically, they overwinter in the egg stage, hatch in early summer, undergo simple metamorphosis, molting four to six times (most commonly five) before reaching the adult stage. Certain species overwinter as late-instar nymphs, but this trait is not simulated in this model. Eggs are laid in the ground or in clumps of grass in pods containing 4–30 eggs, depending on species and nutritional status of the grasshopper. Females continue producing eggs at regular intervals throughout their life, given the availability of adequate food. Fecundity does not appear to drop as females age, at least during the first 60 days of adult life in laboratory colonies of *Melanoplus sanguinipes* (Smith, 1968; Pfadt and Smith, 1972; Fielding, unpublished data). Embryological development is halted upon entering diapause, which prevents the egg from hatching at inopportune times, such as late summer, when it is too late for a second generation to complete development. Where the season is long enough for a full or partial second generation, diapause may be facultative. Diapause is terminated by exposure to cool temperatures for several weeks (Parker, 1930; Church and Salt, 1952).

Grasshoppers of temperate, semi-arid grasslands must cope with a highly variable environment. Environmental conditions, such as precipitation, food quality, temperature, and season length, can vary greatly from year-to-year in temperate grasslands (Blaisdell, 1958; Haferkamp et al., 1993; Knapp and Smith, 2001). Food quality can have a strong influence on growth rate, survival, and fecundity (Pfadt, 1949; Pickford, 1962; Bernays and Chapman, 1973; Joern and Behmer, 1997, 1998). The overall suitability of a host plant for grasshopper growth and reproduction may be determined by a variety of factors, such as protein content, amino acid balance, digestible carbohydrates, or presence/absence of secondary compounds (Thompson, 1999), but regardless of the particular factors involved, it is clear that quality of food plants will vary spatially, and temporally, within season and between seasons (Thorhallsdottir, 1990; Oedekoven and Joern, 2000; Knapp and Smith, 2001).

Food limitation implies intraspecific competition. There is diverse indirect and direct evidence that populations of some species of grasshoppers in semi-arid grasslands of North America are at least occasionally limited by available food resources. Kemp and Cigliano (1994) collected fewer species of grasshopper in samples taken during drought years. There is a positive correlation between grasshopper populations and precipitation in more arid regions of the western United States (Capinera and Horton, 1989; Fielding and Brusven, 1990). Populations of *Melanoplus sanguinipes* were negatively correlated with livestock grazing, except during a year of above-normal precipitation when net primary production was greater (Fielding et al., 2001). By manipulating grasshopper numbers and food resources within cages, Belovsky and Slade (1995), Joern and Klucas (1993), Oedekoven and Joern (2000), and Branson (2003) provided direct experimental evidence of food limitation in common species of grasshoppers in semi-arid grasslands. It is not clear whether the nature of the competition is primarily exploitative or interference. Results of Branson (2003) indicate primarily exploitative competition. Belovsky and Slade (1995) commented that the competition observed in their experiments appeared to be primarily exploitative, but also, that evidence from other studies suggests that interference competition may be operating, with larger grasshoppers able to more successfully obtain and defend food resources (Wall and Begon, 1986; O'Neill et al., 1993).

1.2. Life history trade-offs

Size of offspring (or eggs) is a trait that may have significant influence on an organism's fitness (Roff, 1992). If growth rate is the same regardless of egg size, and adult size is fixed, larger offspring will require less time to reach maturity. Larger offspring require a greater investment of resources (e.g., protein, lipids) per offspring, meaning that fewer offspring can be produced at a given rate of resource assimilation. Thus, there is a potential trade-off between early maturity

(larger offspring) and number of offspring. All else being equal, larger eggs, and thus shorter juvenile development times, are favored when juvenile development is slow and juvenile mortality is high. Smaller eggs, and thus more offspring per adult, are favored by more rapid juvenile growth rates and shorter adult life-span. Sibly and Monk (1987) analyzed this trade-off with a mathematical model derived from grasshopper data, using constant juvenile and adult mortality rates. In populations affected by intraspecific competition and variable food resources, growth rates and survival will vary among individuals depending on competitive interactions among individuals and spatially variable levels of resource quality and quantity.

Age and size at maturity are other life history traits with similar trade-offs as for egg size. As environmental conditions deteriorate and growth rate slows, it is common for grasshoppers and other arthropods to molt to the adult stage at weights less than their genetic potential (Dean, 1982; Higgins and Rankin, 1996; Ashby, 1997; Tatar et al., 1997; Higgins, 2000; Flanagin et al., 2000). Several authors have analyzed plastic responses of body size and generated predictions regarding optimal reaction norms of age and size at maturity under differing environmental conditions (Stearns and Koella, 1986; Nylin et al., 1996; Tenhumberg et al., 2000; Day and Rowe, 2002). Many analyses assume a positive relation between size at maturity and fecundity (Roff, 1992). Although this assumption is not always valid (Klingenberg and Spence, 1997), it is common enough to form the basis for the following simulations of evolution of reaction norms of age and size at maturity.

Environmental conditions for grasshoppers, such as food quality or quantity, or density of conspecifics or competing species, vary greatly over space and time and this heterogeneity may have important consequences for a species' population dynamics and life history evolution (Collett et al., 1998; Day, 2000). The greatly increased mobility of adults is another factor contributing to the selection pressures influencing optimal age at maturity. If resources are limited and high grasshopper densities cause strong competition for resources, greater mobility will enable grasshoppers to find areas where resources are more plentiful. The spatial arrangement of such resources and grasshopper populations will influence the relative benefits of high mobility.

1.3. Modeling approach

An individual-based approach was used because intraspecific competition arises from localized interactions among individuals. Traditional state-variable models either ignore individual variability or can treat it only indirectly (Uchmanski and Grimm, 1996). Analysis of models comprised of populations of discrete individuals can lead to different conclusions than those arrived at from treating populations as continuous densities (Durrett and Levin, 1993; Wilson, 1998; Uchmanski, 2000). The potential advantages of IBMs come from their bottom-up approach where population-level phenomena emerge from the behavior of individuals and from interactions among those individuals (Grimm, 1999; Railsback, 2001). Spatially explicit IBMs allow the effects of localized interactions and demographic stochasticity to be simulated (Caswell and John, 1992; Wilson, 1998). IBMs also allow simulation of more realistic details of an organism's biology and environment. Most analyses of life history trade-offs have used population averages in differential equations (Roff, 1992). More recently, ecologists have begun to explore the use of IBMs to analyse evolutionary processes in a variety of systems (Scheiner, 1998; Rees et al., 1999; Warren and Topping, 2001; Strand et al., 2002).

Most previous simulation models of grasshoppers have been at the population level (Gyllenberg, 1974; Rodell, 1977; Mann et al., 1986; Hardman and Mukerji, 1982; Berry et al., 1995). Additionally, most of the previous modeling efforts have focussed on only one or two aspects of grasshopper population ecology, such as weather (Carter et al., 1998), or have not simulated dynamics beyond a single year (Berry et al., 1995). Carter et al. (1998) developed a model wherein individuals in the egg stage were explicitly modeled for the purpose of simulating the process of embryological diapause. Schmitz and Booth (1997) and Schmitz (2000) used an IBM loosely based on grasshopper biology to examine the persistence of food chains and to elucidate the level of detail required to predict population and community-level dynamics. Berger et al. (1999) used an IBM to assess the accuracy of different sampling methodologies for the study of grasshopper mobility.

In this model, availability and quality of food limits grasshopper growth and fecundity. Grasshoppers may

escape local depletion of resources by random movements. The propensity to move is an inverse function of the individual's rate of resource assimilation. Certain attributes of individuals, for instance, size of offspring, are represented by real-valued 'genes' which are inherited from their parents. Differential survival and reproductive success by individuals possessing different traits allows the frequency of the more fit attributes to increase and eventually dominate the population. Many analyses of life history traits assume that offspring of larger individuals will have greater survival and/or faster rates of growth (e.g., Stearns and Koella, 1986; Sibly and Monk, 1987). In this paper, no costs are imposed on smaller offspring except those which arise from competitive interactions or foraging capability.

1.4. Objectives

The first, preliminary, objective was to assess the congruence of solutions evolved by simulation with those obtained by mathematical analysis of two life history traits, optimal egg size and reaction norms of size at adult molt. As each feature was added during the development of the IBM, it was tested and output examined to ensure that it was functioning as intended. Nevertheless, errors due to programming flaws or mistaken assumptions may be difficult to identify because of the complexity which is typical of IBMs (Railsback, 2001). If the model is parameterized to match the assumptions of traditional mathematical models as nearly as possible by specifying, for example, constant mortality rates, a spatially uniform environment, constant growth rates within a season, and unlimited food, it should produce results similar to those obtained from the mathematical analysis. The effects of demographic stochasticity in the IBM may introduce some variability in the results, but, with a large population size, and repeated runs, differences in solutions should be slight. Congruence of results between the two methods would lend some confidence in results obtained by the IBM under more biologically realistic details and assumptions.

The second, and primary, objective was to examine how intraspecific competition and spatial structuring of resources may influence the selection pressures acting on the evolution of life history traits. For this objective, food was limited and growth rates were determined by the amount consumed and assimilated. The model was used to compare optimal egg size and reaction norms of age and size at maturity under combinations of type of competition (exploitative or size-based interference), and three degrees of spatial heterogeneity in resource quality.

2. Model description

The model was coded in C++, taking advantage of that language's object-oriented features. Object classes in the model included grasshoppers, cells (discrete spatial units), and a landscape (a rectangular grid of cells). Conceptually, the model consisted of individual grasshopper objects which hatch, consume resources, grow, reproduce, move about, and die within the landscape. All conversions of energy and matter from plant to grasshopper were expressed as gravimetric measures, relative to the size of the grasshopper ($mg\,mg^{-1}$ grasshopper biomass). Growth rates of grasshoppers were determined by the amount of food consumed and its quality or assimilation rate. All populations were univoltine with non-overlapping generations. Details of the model varied according to the objectives of the simulation, but a general description of model follows. Default values for parameters are shown in Table 1.

2.1. Grasshoppers

Each grasshopper possessed the following attributes: age (days after hatch); stage of development (egg, nymph, or adult); somatic mass; reproductive mass; mean daily growth rate (3-day running mean); and location on the landscape (x, y coordinates). In addition, each grasshopper possessed 'genes' that determined the mass of any eggs it produced and three parameters of a power function that determined the reaction norm of adult size as a function of mean daily weight gain.

2.1.1. Growth and development

Embryonic diapause was obligatory, that is, no eggs hatched until the year after they were produced. All eggs hatched on the first day of the season. The initial weight of newly hatched individuals was equal to the weight of the egg from which it developed, which was

Table 1
Parameters and default values, if any, used in the models

Parameter	Description	Default values	Relevant equations
w_t	Weight (mg dry weight) of individual at time, t (days)	–	Eqs. (1) and (4)
w_a	Weight at maturity (mg dry weight)	100.0	Eqs. (3), (9) and (10)
z	log egg weight	–	Eq. (8)
a_0, a_t	Assimilation rate (food quality) at beginning of season, and on day t	0.215	Eqs. (1), (2) and (7)
c_t	Consumption rate (mg food mg^{-1} grasshopper)	0.530	Eqs. (1), (2) and (4)
l	Respiratory loss (mg mg^{-1} grasshopper)	0.034	Eq. (1)
k_t	Growth rate $= (ca - l)$	0.080	Eqs. (8), (9) and (10)
$k_{(3)}$	3-day running mean growth rate	0.080	Eqs. (3) and (5)
q_t	Proportion of plant material within a cell consumed by grasshoppers	–	Eq. (7)
r_t	Ratio of grasshopper:plant biomass within a cell	–	Eq. (4)
A, B, C	Evolvable parameters determining weight at maturity	–	Eq. (3)
s	Scaling factor	100	Eq. (3)
μ_e, μ_j, μ_a	Daily mortality rate for eggs, juveniles, adults	0.01	Eqs. (6), (8) and (10)
n_t	Number of grasshoppers within a 9-cell neighborhood at time	–	Eq. (6)
N	Constant	72	Eq. (6)
t_e, t_j, t_p	Duration of egg stage, juvenile stages, and interval between egg pods (days)	–	Eqs. (8), (9) and (10)
T	Season length (days)	120	Eqs. (7), (8) and (10)
p_t	Probability of moving	0.2	Eq. (5)

determined by the mother's gene for egg size (see Section 2.1.3). Default egg size was 1.0 mg.

Because temperature effects were not a focus of this study, growth of nymphs was determined solely by the amount of food consumed and its assimilation rate (i.e., quality):

$$\frac{dw}{dt} = w_t(c_t a_t - l) \tag{1}$$

where w_t is the individual's weight (mg dry weight) on day t, c_t is the amount of food consumed, a_t is the assimilation rate (food quality), and l represents metabolic expenditures (c, a, and l are mg mg^{-1} grasshopper mass). Daily metabolic loss, l, was a constant of 0.034 per day.

Actual grasshoppers may increase consumption of food, up to a limit determined by the capacity of their digestive systems, to compensate for low levels of critical nutrients (McGinnis and Kasting, 1967; Simpson and Abisgold, 1985; Yang and Joern, 1994a,b). Thus, daily food consumption was inversely proportional to food quality, up to a maximum of 80% of their body weight:

$$c_t = \begin{cases} \dfrac{0.1140}{a_t} & a < 0.1425 \\ 0.8 & a \le 0.1425 \end{cases} \tag{2}$$

Grasshoppers continue to accumulate somatic mass until they attain the target weight at which they become adults. The default target weight was 100 mg. In simulations involving the reaction norm of age and size at maturity, the target weight at maturity was a function of mean daily growth rate ($ca - l$).

$$w_a = A + B(sk_{(3)})^C \tag{3}$$

where w_a is the target weight at maturity, $k_{(3)}$ is the 3-day running mean daily growth rate, s is a scaling factor (equal to 100), and A, B, and C are evolvable attributes of each individual. Lower and upper bounds for A, B, and C were -200 to 200, 0 to 1, and 0 to 10, respectively, ranges which allow for a wide variety of shapes and slopes.

2.1.2. Competitive interactions

Intraspecific competition was implemented with two different methods corresponding to interference (based on size) and exploitative competition. Intensity of interference competition increased with increasing grasshopper:plant ratio. A tournament-style process was used to model interference competition. The size of the individual relative to another randomly selected grasshopper from within the same cell was determined. If the individual's relative size was less than a factor determined by the ratio of grasshopper to plant

biomass within the cell, its food consumption for that day was reduced by half. Otherwise, it fed to capacity:

$$\text{If } \frac{w_1}{w_2} < r_t 10, \quad c = 0.5c \quad r < 0.1$$
$$\text{If } \frac{w_1}{w_2} < 1.0, \quad c = 0.5c \quad r \geq 0.1 \tag{4}$$

where w_1 and w_2 are, respectively, mass of the target grasshopper and a grasshopper selected at random from the grasshoppers within the same cell, r is the ratio of grasshopper:plant biomass in the cell, and c is food consumption. Thus, when food resources are abundant relative to grasshopper biomass, nearly all grasshoppers feed to capacity, but as food resources become more scarce, size of the grasshopper becomes more important. When the grasshopper:plant ratio reaches 0.1 and greater, the grasshopper must be at least as large as the randomly selected grasshopper to feed to capacity.

In simulations of exploitative competition, all grasshoppers simply fed to capacity until the food resources within a cell were exhausted or the grasshoppers moved to another cell.

2.1.3. Reproduction

After individuals attain their target size, they become adults and assimilated biomass is no longer allocated towards growth, but towards reproduction. The same function is used for accumulation of reproductive biomass as somatic growth, except the rate of weight gain was divided by a factor of 5 to account for the greater concentration of energy and protein in the eggs and the extra biomass associated with production of a pod. The rate of metabolic loss remains the same.

Grasshoppers were modeled as a parthenogenetic population of females (i.e., all grasshoppers reproduced copies of themselves). After grasshoppers have accumulated enough biomass to produce one or more eggs, they generate as many copies of themselves as the clutch size. In simulations where egg size was allowed to evolve, each individual inherited a characteristic egg size, with lower and upper bounds of 0.1–10 mg. Clutch size is determined by integer division of reproductive mass by egg mass. After new grasshopper objects are created, the equivalent amount of reproductive biomass is subtracted from the mother's total. Remainder reproductive biomass is carried over to the next time step.

When new grasshopper objects are generated, there is a probability of mutation (0.01), which functioned as a source of new gene values during the course of the simulation. When mutation occurred, the value of the parental gene was replaced by a value drawn randomly from a Gaussian distribution centered on the value of the parental gene with standard deviation of 10% of the difference between the minimum and maximum values for that gene.

2.1.4. Movement

Movement by grasshoppers consists of a random walk. Each grasshopper, at each time step, may move with a probability that is a function of mean daily growth rate (Fig. 1):

$$p_t = 0.003 k_{(3)}^{-1.5} \tag{5}$$

If the grasshopper moves, two random numbers uniformly distributed from −1 to 1 were generated, representing proportions of maximum distance moved in east-west and north-south directions. Adults may move a maximum distance of one-half the width of the landscape. Nymphs move a maximum of one cell per day. If the move takes the grasshopper beyond the boundaries of its cell, it is removed from that cell's list and copied into the appropriate cell.

2.1.5. Mortality

Because it is unrealistic to imagine that the sole mortality factor is starvation as a result of intraspecific competition, non-selective background mortality of 0.01 per day was instituted for juveniles and adults. Eggs were subject to a constant mortality rate (default = 0.015 per day). For simulations employing density-dependent background mortality rates, e.g.,
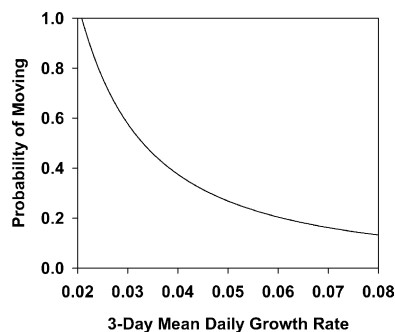

Fig. 1. Probability of an individual moving as a function of its 3-day running mean growth rate.

from predation, the number of individuals within a 3×3 cell neighborhood was determined. A polynomial relation was defined such that the maximum mortality of 0.03125 per day occurs when grasshopper densities reach 1.25 of the maximum density neighborhood density:

$$\mu_{j,a} = \frac{0.05 n_t}{N} - 0.02 \left(\frac{n_t}{N}\right)^2 \qquad (6)$$

where $\mu_{j,a}$ is the background daily mortality rate of adults or juveniles (restricted to values >0), and n_t is number of grasshoppers within the 9-cell neighborhood, N is a constant (default = 72). At higher densities, mortality rate declined to simulate predator satiation.

If little or no food is available, the grasshopper cannot meet its metabolic demands, thus it loses weight (0.034 mg mg^{-1} day^{-1}). If the grasshopper's 3-day running mean growth rate becomes less than 0.005, it dies and is removed from the system. On the last day of season, all nymphs and adults were killed to simulate freezing temperatures. An annual mortality rate of over-wintering eggs was applied once per year (default = 0.05).

2.2. Cells and food resources

Cells are the basic spatial units of the model. Data structures of the Cell class included a linked list of grasshopper objects, number of eggs, nymphs, and adult grasshoppers in the cell, total biomass of nymphal and adult grasshoppers, plant biomass, plant quality, cell rank and file, and pointers to the eight adjacent cells. Grasshopper and plant variables were updated at the beginning of each time step. When a new simulation was initialized, an equal number of grasshoppers was spawned within each cell. These new grasshopper objects were assigned a specific, random location within the cell. Genes of the initial population of grasshoppers were random real numbers uniformly distributed between the upper and lower limits for each gene. At each time step, the grasshopper objects in each cell executed their functions in the following order: feeding and growth, reproduction, movement, and mortality (Section 2.1).

At the beginning of each year, all cells were initialized with the same quantity of plant biomass (default = 4000). As grasshoppers consumed plants

during the year, plant biomass was reduced by a corresponding amount. No new growth of plants occurred during the year. Food quality, a, was uniform within a cell.

Food quality declined during the season, to simulate phenological decline in protein content and increasing non-digestible fiber with plant maturation (Oedekoven and Joern, 2000). Food quality within each cell also declined independently as a function of the amount consumed by grasshoppers, assuming that grasshoppers feed preferentially on higher quality plant tissues first, such as leaves, thus increasing the proportion of less desirable tissues, such as stems. Declining plant quality due to phenological changes and preferential feeding by grasshoppers were combined in an equation that updated plant quality within each cell daily (Fig. 2):

$$a_t = a_0 \left(1 - 0.8 \left(\frac{t}{T}\right)^{1.5}\right)(1 - q^2) \qquad (7)$$

where a_t is food quality on day t, a_0 is food quality at the beginning of the season, T is total season length (default = 120 days), and q is the proportion of plant biomass consumed by grasshoppers.

2.3. Landscapes

The simulations took place on a landscape composed of a square lattice of cells. Landscape
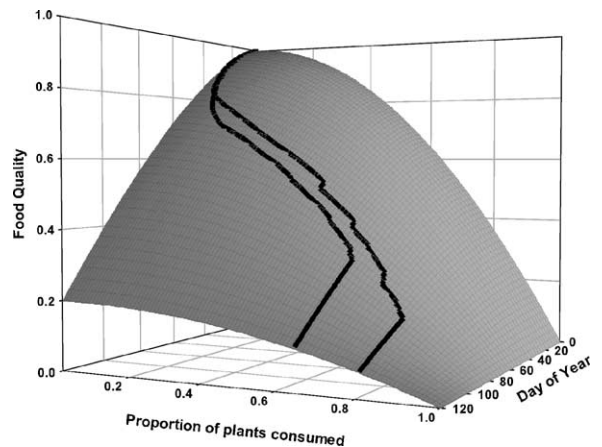

Fig. 2. Proportional decline in food quality from initial value at the beginning of the season as a function of day of year and proportion of plants consumed. Bold lines on the surface are examples of seasonal trajectories in food quality within a cell.
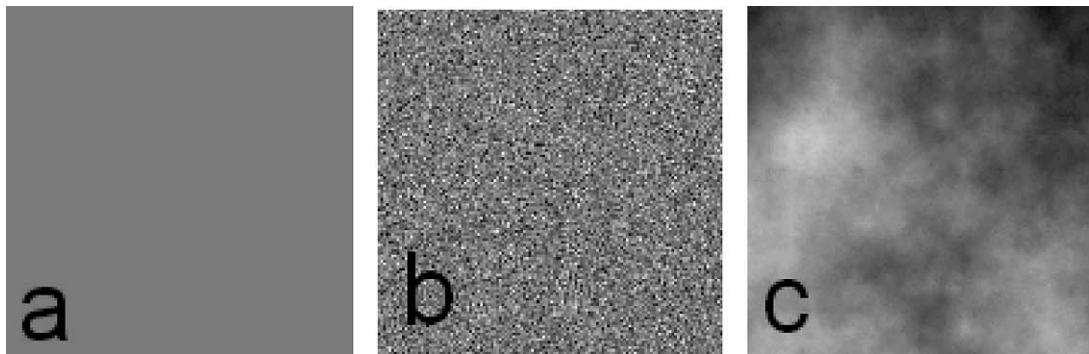
Fig. 3. Examples of the three types of spatial distributions of food quality used in the simulations: (a) uniform; (b) random; (c) fractal. Landscapes are 128×128 cells and show food quality at the beginning of season. Lighter shades indicate higher food quality. Mean food quality is the same for each landscape.

boundaries were periodic, i.e., the lower row of cell borders the upper row and the left-most column of cells are adjacent to the right-most column, forming a torus. Periodic boundaries avoid artifacts associated with edge effects.

In simulations with a uniform distribution of food quality (Fig. 3a), plants in all cells were initialized with same food quality (default value of 0.215). Published data indicate that 0.215 is a reasonable assimilation rate for many plant materials (Bailey and Riegert, 1973; Duke and Crossley, 1975). In simulations with random landscapes (Fig. 3b), plant quality values were drawn randomly from a normal distribution with mean 0.2 and S.D. 0.04. Fractal landscapes (Fig. 3c) were generated with the midpoint displacement algorithm (Peitgen and Saupe, 1988) with a fractal dimension of 2.5. A normal deviate was assigned to each cell. The food quality at the beginning of the season in each cell was determined as the product of the normal deviate and the standard deviation of food quality which was added to the mean value for food quality. The quantity of food in each cell did not vary spatially or annually, with default value of 4000 mg.

3. Comparison of mathematical solutions with simulations

As an assessment of the IBM, two different problems from life history theory were simulated and solutions (population modes) were compared to those obtained by mathematical analysis. Because of the

stochastic elements in the simulation model, results varied among runs. Therefore, multiple runs were made under each of the different model configurations to assess the variance in results. To accurately simulate the mathematical models several simplifying assumptions had to be incorporated into the simulations.

3.1. Evolution of egg size

Sibly and Monk (1987) analyzed the trade-off between duration of the juvenile stage and reproductive potential for three species of univoltine grasshoppers in Britain. Optimal egg size depends on the relationship between egg size, duration of the juvenile period, and fecundity, as well as mortality rates during the adult and juvenile stages. The assumption that larger eggs result in shorter development times has been challenged (Grant et al., 1993), but Sibly and Monk's (1987) model is useful for testing the solutions of the IBM simulations.

3.1.1. Mathematical analysis

The trade-off was analyzed by first defining the relationship between nymphal development time and egg size. A plot of this function defines the boundary between possible and impossible solutions, i.e., an egg of a certain size has some minimum development time. The solution maximizing fitness will lie on this boundary (Roff, 1992). Next, isolines of fitness were calculated as a function of egg size, juvenile development time, fecundity rates, and mortality rates. The

optimal combination of egg size and development time occurs at the point where a fitness isoline is tangent to the plot of egg size versus development time (Roff, 1992).

In the mathematical model developed by Sibly and Monk (1987), fitness was measured as the number of females in the current year per female at the same stage of the previous year (one generation per year). This fitness measure is equivalent to e^F, where F is the instantaneous rate of increase (Sibly and Monk, 1987). The complete mathematical model was derived from consideration of mortality rates of eggs, nymphs, and adults, duration of the nymphal stage, rate of egg production, number of eggs per pod, and duration of the inter-pod interval. Eq. (7) of Sibly and Monk (1987) defines the fitness isolines,

$$z = -F + \log k + \log t_j - \mu_e T + \mu_e t_j - \mu_e t_e$$
$$- \mu_j t_j + \log(1 - e^{(\mu_e - \mu_a)(T - t_j)})$$
$$- \log(1 - e^{(\mu_e - \mu_a)t_p}) \tag{8}$$

where z is log egg weight, F is fitness, k is the rate at which resources destined for egg biomass are accumulated, μ_0, μ_1, μ_2 are daily mortality rates of eggs, nymphs, and adults, respectively; T, t_e, t_j, t_p are duration in days of the entire season, egg developmental period, nymphal development period, and interval between pods, respectively (see Sibly and Monk, 1987, for derivation of equation).

Sibly and Monk (1987) did not define the relationship between log egg size and nymphal development period, $z(t_1)$, except to describe it as non-linear and concave when viewed from above. In my simulations, nymphal development times were determined by growth rate and the body weight at which nymphs transform into adults, and so $z(t_1)$ could be precisely defined. Under the conditions of the simulation model, rate of growth of nymphs was constant resulting in exponential weight gain by nymphs. Therefore, nymphal developmental time decreased linearly with increasing log egg size.

3.1.2. Simulation

Simplifications were made to the simulation model to reflect the assumptions of the Sibly and Monk (1987) model. Because results would be affected by variable, density-dependent juvenile and adult mortality, food was unlimited and combinations of constant mortality rates were used that allowed the population size to remain fairly constant over at least 50 generations. Relative food consumption, c, was constant (0.53). The interval between pods, t_p, was constant at 5 days. With a constant interval between pods, the number of eggs per pod varied according to the size of the eggs.

Simulations were run under two combinations of adult and nymphal mortality rates: low nymphal, high adult mortality ($\mu_e = 0.028$, $\mu_j = 0.039$, $\mu_a = 0.065$); and high nymphal, low adult mortality ($\mu_e = 0.002$, $\mu_j = 0.052$, $\mu_a = 0.018$). Growth rate was constant at 0.08. All runs were made with a total season length of 90 days (from egg hatch to the end of the season). Simulations were run with an initial population of 10,000 individuals on a uniform landscape of 20×20 cells. Genes for egg weight in the initial population were uniformly randomly distributed between 0.01 and 10.0 mg. All other genes were static. Adult size was set at 100 mg (dry weight). Egg weights were converted to nymphal development times using the appropriate log-linear functions, $z(t_1)$, to compare with results of the mathematical analysis.

3.1.3. Results

The simulation typically converged to a solution within 20 generations. Solutions found by different runs of the IBM simulations spanned a range of viable solutions (Fig. 4) that differed only slightly in their level of fitness. As expected, evolved egg size was larger (and t_j less) under conditions of high juvenile mortality (Fig. 4a), and eggs were smaller (and t_j greater) under high adult mortality (Fig. 4b).

3.2. Evolution of phenotypic plasticity

In these simulations, egg size was held constant (1 mg) and the parameters controlling size at maturity were allowed evolve. Food quality was constant within a season and among cells. Food quantity was unlimited.

3.2.1. Mathematical analysis

A simple mathematical model was used to determine optimal size at maturity as a function of growth rate. I used the number of eggs surviving at the end of the season per female as a measure of fitness, R_o. Fitness was calculated as the summation of the daily
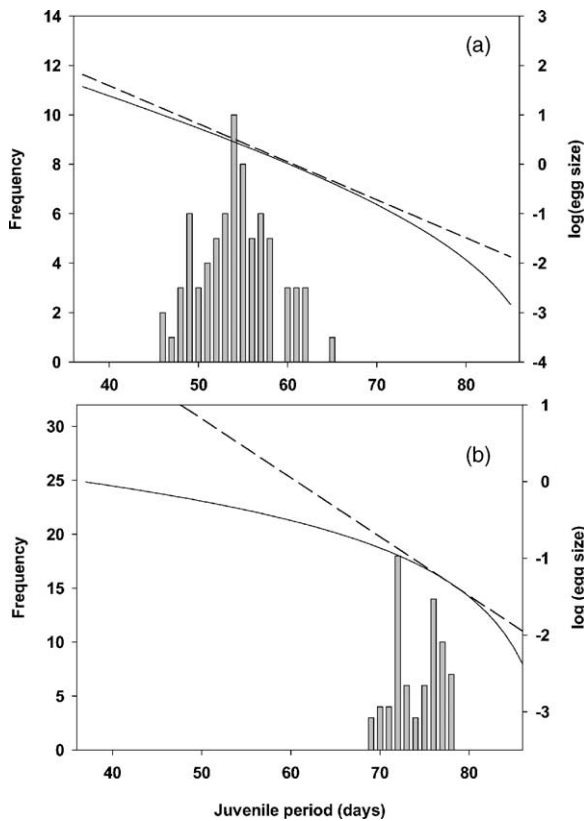
Fig. 4. Frequency of evolved juvenile developmental times (population modes) from 80 runs of the model (bars). Juvenile developmental times are determined by egg size. The dashed line represents the range of possible solutions. Solid lines represent fitness isolines (Sibly and Monk, 1987). Optimal juvenile development time is at the point where a fitness isoline is tangent to the line of possible solutions. (a) Egg, juvenile, and adult mortality = 0.028, 0.039, and 0.065, respectively; (b) egg, juvenile, and adult mortality = 0.002, 0.052, and 0.018, respectively.

product of fecundity of adult grasshoppers, expected survival of adults, and expected egg survival from oviposition to the end of the season. Because growth occurred in discrete daily time-steps, the duration of the juvenile period was calculated using the discrete time formula:

$$t_j = \frac{\log_e w_a}{\log_e(1 + k_t)} \tag{9}$$

where t_j is time required for juvenile development, w_a is size at maturity, and k is the daily growth rate. Daily fecundity was calculated as the product of adult

weight and daily fertility rate (growth rate divided by 5, see Section 2.1.3). Survival of eggs was calculated from daily mortality rate of eggs ($\mu_e = 0.015$) and the time from oviposition to the end of the season ($T - t$). Juvenile and adult survival was calculated from daily mortality rates, $\mu_a = 0.035$ and $\mu_j = 0.035$, for adults and juveniles, respectively.

$$R_o = \sum_{t=1}^{T} e^{-\mu_a(t-t_j) - \mu_j t_j - \mu_e(T-t)} w_a \frac{k_t}{5} \tag{10}$$

As growth rate decreases, individuals require more time to attain a given adult size and larger adult sizes become less fit because fewer individuals survive the extended juvenile development period and the remaining time available for reproduction is shortened. As growth rate increases, faster juvenile development allows relatively more time for larger adults to take advantage of their greater fecundity. Optimum adult size for different growth rates was determined by solving Eq. (10) for adult sizes from 10 to 200 mg, at 1 mg increments. Adult size that gave the highest value of R_o was considered the optimum size. This was repeated for growth rates from 0.060 to 0.090 to generate an optimum reaction norm.

3.2.2. Simulation

Examination of the predicted reaction norm for optimum adult size suggested that it could be most accurately modeled as a power function. Therefore, realized adult size for each individual in the simulation was determined as in Section 2.1.1.

Ten runs each were made with a constant growth rate of 0.08 and with annually variable growth rates. Values of *a* were constant over time and space (uniform landscape) within a year, but varied randomly between years (uniformly distributed between 0.177 and 0.234). Relative food consumption, *c*, was constant (0.53). This resulted in daily growth rates from 0.060 to 0.090. Mortality rates for eggs, juveniles, and adults were set at 0.015, 0.035, and 0.035, respectively. The simulation was initialized with a population of 10,240 individuals evenly distributed over a 32×32 cell landscape. Non-selective, density-dependent mortality of the over-wintering eggs kept the population under 15,000 individuals. The simulations were allowed to run for 100 generations. Because different combinations of the evolvable parameters *A*, *B*, and *C*

in the function determining size at maturity (Eq. (3)) could result in similar reaction norms, the population mean reaction norm was extracted by calculating the size at maturity (using Eq. (3)) for each individual of the 100th generation at seven growth rates between 0.06 and 0.09 and plotting the mean values and standard deviations.

3.2.3. Results

The fitness function (Eq. (10)) for non-varying growth rate of 0.08 had a stepped response because of the discrete daily time step (Fig. 5). Within each daily time step, fitness increased up to the maximum adult size that could be attained within that time step, resulting in a function with a series of local optima. With a constant growth rate of 0.08 ($a = 0.22$), the modal value for adult size in the simulated population did not precisely match the optimum found by mathematical analyses (Fig. 5), however, there was very little difference in fitness among the top several local optima and the simulated population showed peaks in gene frequencies that matched those local optima. With annually variable growth rates, the median evolved reaction norm fell within the range of 95% of optimal fitness as defined by Eq. (10) (Fig. 6). The population mean reaction norm was not as steep as the predicted norm. Size at maturity increased with growth rate, but age at maturity remained relatively constant.

4. Effects of intraspecific competition and spatial heterogeneity

In these simulations, the simplifying assumptions of constant mortality, spatial homogeneity, and constant within-season growth rates were supplanted with mechanisms arising from the interactions of individuals with each other and their environment. Populations were limited by food resources, rather than by externally imposed mortality rates. As above, growth rate was determined by food quality, but instead of remaining constant, food quality declined seasonally as described in Section 2.2 (Eq. (7)). Typical seasonal trajectories of food quality are shown in Fig. 2, however, there was a great deal of variation in food consumption among cells depending on the numbers of grasshoppers. Individuals were able to compensate for poor quality food by increasing consumption up to 0.8 of their somatic mass (Eq. (2)). Grasshoppers were also more likely to move to other cells as growth rate declined (Eq. (5)). Intraspecific competition was simulated with different methods corresponding to exploitative and interference competition (Section 2.1.2). To test whether the effects of intraspecific competition persisted with externally imposed density-dependent factors, e.g., predation, simulations were also conducted with density-dependent mortality (Eq. (6)).

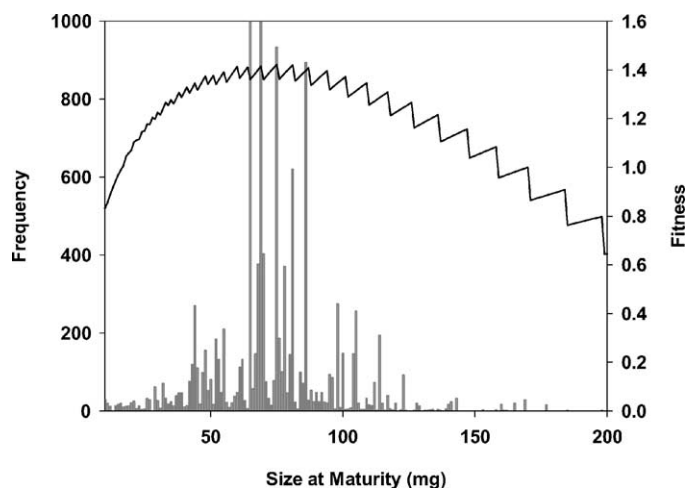All simulations took place on a 128×128 grid and allowed to run for 100 generations. The spatial

Fig. 5. Calculated fitness of different adult weights (solid line) and evolved gene frequencies after 100 generations (bars) with daily growth rate (0.08) constant between years.
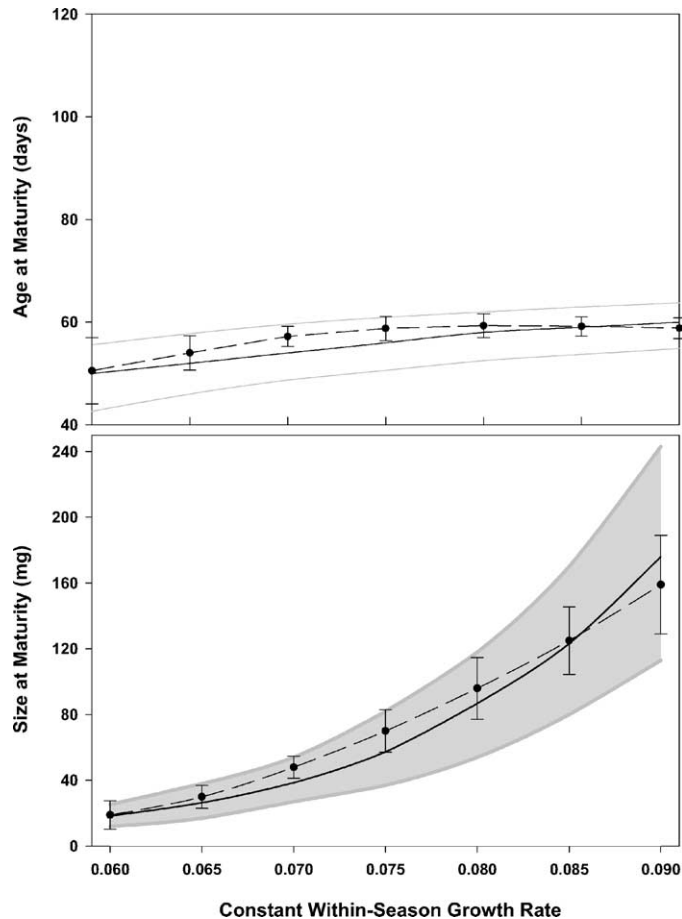
Fig. 6. Calculated optimal adult weights (solid line) as a function of growth rate and median evolved reaction norm (dashed line) of population after 100 generations. Thin grey lines denote limit of values with fitness of at least 95% of calculated optimum.

arrangement of food quality varied from uniform to random to a spatially autocorrelated pattern, but the mean value of food quality across the landscape at the beginning of each season did not vary. The initial quantity of food in each cell did not vary annually. Ten simulations were run for each combination of nature of competition (interference, exploitative), spatial heterogeneity of food quality (uniform, random, fractal), and background mortality (constant, density dependent).

4.1. Egg size

Egg size was allowed to evolve in these simulations. Adult size was held constant (100 mg) and season length was 120 days. Differences in modal egg size among the different sets of conditions was tested with ANOVA.

Because the interaction effects of background mortality with competition and spatial structure were highly significant, a separate ANOVA was conducted for constant mortality and density-dependent mortality. In the simulations with constant mortality, type of competition and spatial structure were both highly significant (F-values >130, $P < 0.001$), whereas under density-dependent mortality, only competition was significant ($F = 89$, $P < 0.001$) and the effect of spatial structure was completely lost ($F = 0.29$, $P = 0.75$). Larger egg sizes were evolved under interference competition in each combination of spatial structure and mortality (Table 2) reflecting the

Table 2
Mean[a] (S.D.) of modal gene values for egg size from 10 simulations for each combination of landscape, competition, and background mortality

Competition type	Uniform landscape	Random landscape	Fractal landscape
Constant background mortality			
Exploitative	2.75d (0.097)	2.68d (0.132)	3.95b (0.275)
Interference	3.57c (0.170)	3.42c (0.103)	4.55a (0.450)
Density-dependent background mortality			
Exploitative	2.14a (0.084)	2.15a (0.127)	2.09a (0.209)
Interference	2.56b (0.158)	2.47b (0.116)	2.58b (0.253)

[a] Means within types of background mortality followed by the same letter are not significantly different ($P > 0.05$, LSD test).

selection pressure associated with size-based interference competition. Under constant mortality, populations on fractal landscapes also evolved larger eggs (Table 2). In no case did egg size differ between uniform and random distribution of resources. In every case, egg sizes were smaller in simulations with density-dependent mortality than in the corresponding set of conditions with constant mortality (Table 2), indicating that the external density-dependent mortality factor, such as predation, reduced the intensity of competition and created enough low density cells such that the advantage of long distance foraging by adults on fractal landscapes was not enough to affect egg size.

4.2. Reaction norm of age and size at maturity

Egg size was held constant at 1.0 mg and a plastic response of size at maturity was allowed to evolve in these simulations. The mean reaction norm was extracted from the population as described in Section 3.2.2. Mean values of realized age and size of all individuals surviving to maturity in the 100th generation, and the 3-day mean growth rate at time of maturity, were calculated for each run (Table 3).

With all combinations of landscape structure and background mortality, grasshoppers under exploitative competition tended to reach maturity at an earlier age and smaller size, and before growth rates had declined significantly, compared to those under interference competition (Table 3). The effect of landscape structure was not as consistent, but on the fractal landscapes, size at maturity was less and, at least

Table 3
Mean (S.D.) ages, weights, and growth rates at maturity for all individuals of the 100th generation surviving to adult stage ($N > 10,000$ for each mean)

	Age	Weight	Growth rate
Constant mortality, uniform landscapes			
Exploitative	57.4 (10.56)	78.8 (41.16)	0.074 (0.0111)
Interference	60.6 (10.36)	89.8 (31.98)	0.068 (0.0161)
Constant mortality, random landscape			
Exploitative	53.8 (8.71)	54.1 (23.40)	0.069 (0.0133)
Interference	64.4 (11.20)	79.4 (25.37)	0.061 (0.0185)
Constant mortality, fractal landscape			
Exploitative	54.8 (10.12)	41.1 (24.15)	0.061 (0.0157)
Interference	58.3 (6.41)	45.0 (19.64)	0.049 (0.0199)
Density-dependent mortality, uniform landscape			
Exploitative	57.2 (7.75)	62.8 (21.64)	0.071 (0.0076)
Interference	62.0 (8.06)	80.8 (21.06)	0.064 (0.0150)
Density-dependent mortality, random landscape			
Exploitative	59.0 (8.52)	64.0 (23.72)	0.065 (0.0139)
Interference	64.4 (9.72)	79.2 (24.19)	0.060 (0.0170)
Density-dependent mortality, fractal landscape			
Exploitative	55.9 (10.39)	59.8 (35.74)	0.062 (0.0124)
Interference	63.9 (10.71)	71.6 (29.63)	0.056 (0.0194)

with constant background mortality, age at maturity was earlier. The standard deviations of age, size, and growth rate under exploitative competition were consistently lower than those under interference competition (Table 3), indicating that unless individuals reached maturity before food resources had deteriorated significantly, they probably would never reach maturity.

The reaction norms of age and size at maturity (Figs. 7 and 8) were qualitatively different than those evolved under the simplified conditions of constant mortality, and constant within-season growth rates (Fig. 6). Under the simplified assumptions, age at maturity was relatively constant and size at maturity was a concave (looking down) function of growth rate, whereas with food limitation, age at maturity was either decreasing, increasing, or relatively constant, depending on the spatial structuring of food resources, and reaction norms of size at maturity were nearly linear. Type of competition had a profound effect on the reaction norms. The magnitude of the standard deviations indicate the severity of selection pressure at different growth rates, with smaller variance indicating stronger selection pressures (Fig. 8).
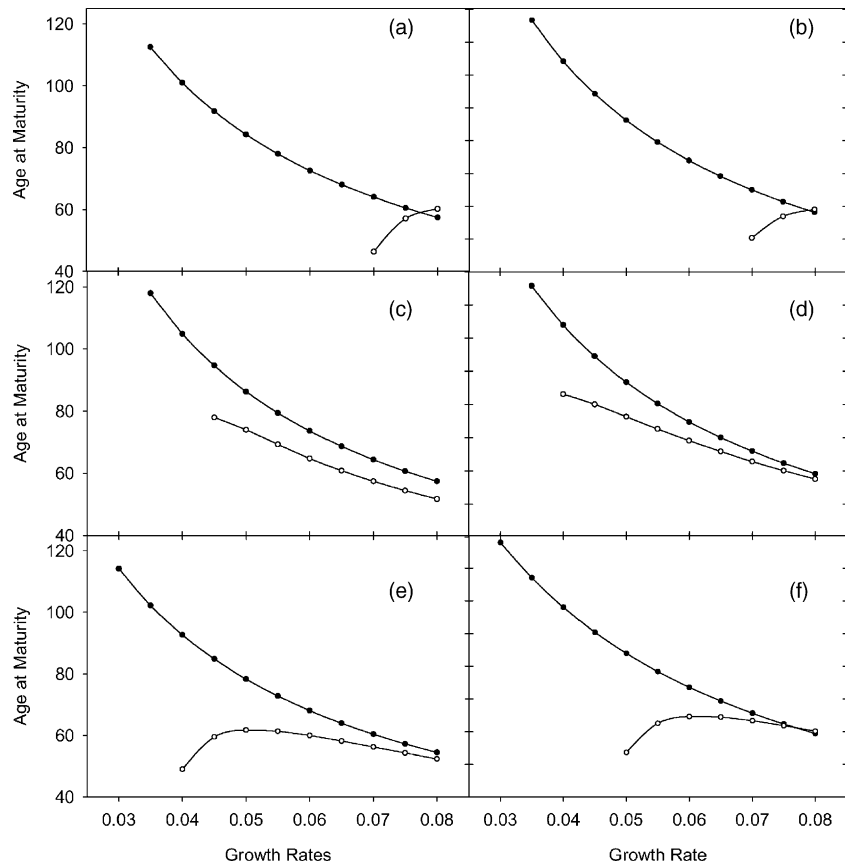
Fig. 7. Mean ($n = 10$) of modal reaction norms of age at maturity. Solid circles, interference competition; open circles, exploitative competition. (a, b) Uniform landscape; (c, d) random landscape; (e, f) fractal landscape. (a, c, e) Constant background mortality; (b, d, f) density-dependent background mortality.

Under interference competition, reaction norms were all very similar qualitatively, with increasing size and decreasing age with higher growth rates. With fractal distribution of resources and interference competition, overall size at maturity was somewhat smaller, especially at lower growth rates (Fig. 8). In contrast, under exploitative competition, landscape structure had a great effect on evolved reaction norms. With a uniform initial distribution of resources, age and size increased steeply with increasing growth rate (with large variance), but only within a small range at the highest growth rates could viable combinations of age and size evolve (Figs. 7 and 8). Under random distributions of resources, age at maturity declined as size increased. On fractal landscapes, age at maturity was

relatively constant (earlier at low growth rates, but from Table 3, it appears that few individuals survived to maturity after growth rates had declined to 0.05 or less), whereas size increased with increasing growth rates (Figs. 7 and 8). With density-dependent background mortality, evolved sizes at maturity tended to be greater, at least at higher growth rates, reflecting less intense competition. Population mean ages and weights in Table 3 did not necessarily correspond to those expected from the reaction norms of Figs. 7 and 8 because growth rates were fluctuating daily for individuals as food was depleted within cells and they moved in and out of cells with more or less food, and other individuals moved in and out of their cells.
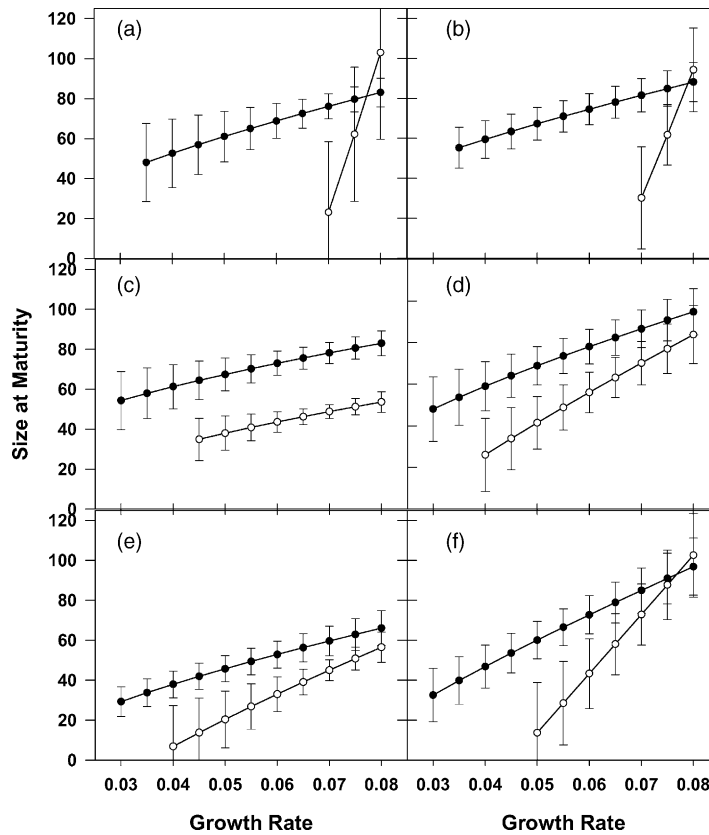
Fig. 8. Mean ($n = 10$) of modal reaction norms of size at maturity. Symbols and arrangements as in Fig. 7. Error bars indicate 1 S.D.

5. Discussion and conclusions

The results of these simulations show that the nature of intraspecific competition and spatial structure of the environment have the potential to strongly influence the evolution of key life history traits in food limited populations. Spatial structuring and interference competition acted on egg size in the same direction, but through different mechanisms. Larger offspring have a competitive advantage in size-based competitive interactions, and, with spatial clumping of resources, earlier age at maturity allows individuals the mobility to find underutilized resources in other cells before food limitation becomes too extreme. For the same reasons, spatial structuring and interference competition acted on size at maturity in opposite directions. Individuals that grew to a larger size more successfully competed for resources during

their reproductive phase and had greater fecundity, but were at a disadvantage on a fractal landscape when resources within their neighborhood were depleted.

Both life history traits, size of offspring and size at maturity, affect the duration of the juvenile stage, i.e., age at maturity. Traditional models have analyzed the selection pressures affecting these traits as a trade-off between early maturity and fecundity. Larger offspring or smaller adults require less time to attain a given weight at the expense of lower fecundity. The optimal balance between these trade-offs has been considered to be, directly or indirectly, a function of adult and juvenile mortality, growth rates, season length, and fecundity (Stearns and Koella, 1986; Sibly and Monk, 1987). The IBM described in this paper incorporates these factors but also allows a richer set of interactions and constraints to be explored.

One of the primary differences between this IBM and previous models is the variability of within-season growth rates. Grimm and Uchmanski (2002) illustrated the importance of within-season density-dependent processes on population persistence. Very few models of evolution of size and age at maturity have considered the effects of within-generation variability of growth rates. Tenhumberg et al. (2000) used a stochastic dynamic programming model to analyse the effects of random variation in food availability on reaction norms of size and age at maturity of syrphid flies. When food availability, and thus growth rates, was low, larvae took the time to grow larger when food supply was constant and predictable, but when food supply was unpredictable, larvae matured earlier and smaller. Although the specific effects of variability in food supply was not a focus of this study, food quality and quantity, and thus growth rates, did vary within a season. Food quality in these simulations was not wholly unpredictable: quality declined steadily and predictably throughout the season, but the amount of feeding by grasshoppers accelerated the loss of food quality. As grasshoppers moved about, individuals could move into cells that contained better or worse food resources, or more grasshoppers could move into an individual's cell, hastening the loss of food quality.

Two mechanisms allowed individuals to buffer the effects of declining food quality. By increasing consumption, grasshoppers were able to compensate for lower food quality. Thus, food quality did not affect growth rates until it reached a low level (about 33% less than the average quality at the beginning of the season). Secondly, grasshoppers increased their foraging efforts (random movements) as their rate of weight gain declined, and thus increased their chances of finding a cell with better food resources. In the uniform and random landscapes, long distance foraging by adults would have little additional benefit over the short distances that nymphs were capable of. This is reflected in the larger eggs and smaller adults that evolved on the fractal landscapes.

At the levels simulated in these runs, the imposition of density-dependent background mortality did not have a large effect on the qualitative patterns of age and size at maturity, and the effects of type of competition on egg size did not change greatly. Obviously, if another factor, such as predation, is the key process regulating populations, then that factor will

have greater impact on life history traits. In nature, it seems probable that the importance of food limitation and predation will vary from year to year. In these simulations, quantity of food and background mortality did not vary annually, but the results suggest that a modest level of top-down density dependence will not greatly alter the selection pressure of intraspecific competition.

Grimm (1999) emphasized that, even though IBMs usually incorporate more realistic details of a system, to be useful IBMs should include only enough detail to capture the essence of the problem to be simulated. The difficulty lies in how much is enough detail. The evolved adult weights at the higher growth rates were similar to that of many grassland acridids (80 mg dry weight) (Pfadt, 1994). Egg size was probably unrealistically high in many cases, suggesting that there may be physiological constraints to egg size or that some of the biological or implementation details need to be reconsidered. In this paper, the objective was a qualitative assessment of selection pressures, or direction of selection, acting on the selected life history traits. Accordingly, the simulations contained many simplifications. Simulations did not include genetic realism: modeled traits were 100% heritable, reproduction was parthenogenic, and no attempt was made to model genetic architecture (Scheiner, 1998). Plant resources declined steadily throughout the growing season. In real life, plants may be revitalized by rainfall, or there may be a progression of different plant species with different phenologies. Season length and temperatures did not vary.

Other details of acridid physiology that may influence the evolution of life history traits, but were not included in these simulations include stages at which size at maturity is fixed and critical threshold size. Flanagin et al. (2000) showed that nymphs of *Romalea microptera* lost their plasticity, in terms of adult size, by the fifth instar. Even though *Romalea* spp. are not inhabitants of semi-arid grasslands, it seems likely that most acridids would, at some point in their ontogeny, lose plasticity with regards to size at maturity. Also, it is likely that each species of grasshopper has some minimum threshold size below which they cannot successfully molt to the adult stage. Results of Day and Rowe (2002) suggest that such a threshold could affect norms of reaction qualitatively. Time limitations precluded the exploration of the effects of

such thresholds, but these effects are worth examination in the future.

There also implementation details that may have had some effect on the results. For instance, the point at which starvation occurred, or the use of a 3-day running mean of growth rate. In the case of phenotypic plasticity, the ability of the virtual grasshoppers to evolve an optimal solution depends on selecting the appropriate type of equation to model the plastic response, e.g., exponential or sigmoid functions. This is not a problem if mathematical analysis or some a priori knowledge indicates an appropriate model, but in cases where the shape of the plastic response is unknown a method is needed to evolve an appropriate equation. One possibility would be to create several competing species, each of which incorporates a different type of equation. The species with the equation that best fits the optimal reaction norm would eventually dominate.

Similarly, events in the simulation occur in discrete time steps, limiting the temporal resolution of the evolved solutions. For example, the optimal juvenile development period may be some fraction of a day but the simulated grasshopper objects can only develop in units of one discrete daily time step. This may not be too far from the natural situation, where diurnal fluctuations in temperature prevent certain physiological functions, such as molting, from occurring during cooler periods of the day. For most applications, time steps of less than 1 day probably would not greatly increase our understanding of the problem at hand.

5.1. Conclusion

Joern and Gaines (1990) suggested that understanding the evolution of life histories in grasshoppers may allow for the prediction of population responses to environmental perturbations by species with different life history traits. The model described here represents a first step towards developing a framework for understanding the multiple factors that influence grasshopper life history evolution and subsequent population dynamics. Although not enough detailed information is available to parameterize the model such that it generates precise predictions of egg size or age and size at maturity for any particular species, results with the current version of the model reinforce the importance of understanding intraspecific competition, and the

particular form it takes, in shaping life histories. Also, the spatial distribution of resources, relative to the dispersal abilities of individuals, may have the potential to alter the selection pressures on key life history traits.

Acknowledgements

References

Ashby, P.D., 1997. Conservation of mass-specific metabolic rate among high-and low-elevation populations of the Acridid grasshopper, *Xanthippus corallipes*. Physiol. Zool. 70, 701–711.

Bailey, C.G., Riegert, P.W., 1973. Energy dynamics of *Encoptolophus sordidus costalis* (Scudder) (Orthoptera: Acridiae) in a grassland ecosystem. Can. J. Zool. 51, 91–100.

Belovsky, G.E., Slade, J.B., 1995. Dynamics of two Montana grasshopper populations, relationships among weather, food abundance and intraspecific competition. Oecologia 101, 383–396.

Berger, U., Wagner, G., Wolff, W.F., 1999. Virtual biologists observe virtual grasshoppers: an assessment of different mobility parameters for the analysis of movement patterns. Ecol. Model. 115, 119–127.

Bernays, E.A., Chapman, R.F., 1973. The role of food plants in the survival and development of *Chortoicetes terminifera* (Walker) under drought conditions. Aust. J. Zool. 21, 575–592.

Berry, J.S., Kemp, W.P., Onsager, J.A., 1995. Within-year population dynamics and forage destruction model for rangeland grasshoppers (Orthoptera, Acrididae). Environ. Entomol. 24, 212–225.

Blaisdell, J.P., 1958. Seasonal development and yield of native plants on the Upper Snake River Plains and their relation to certain climatic factors. U.S. Depart. Agric. Tech. Bull. 1190.

Branson, D.H., 2003. Reproduction and survival in *Melanoplus sanguinipes* (Orthoptera: Acridiae) in response to resource availability and population density: the role of exploitative competition. Can. Entomol. 135, 415–426.

Capinera, J.L., Horton, D.R., 1989. Geographic variation in effects of weather on grasshopper populations. Environ. Entomol. 18, 108–114.

Carter, M.R., Macrae, I.V., Logan, J.A., Holtzer, T.O., 1998. Population model for *Melanoplus sanguinipes* (Orthoptera, Acrididae) and an analysis of grasshopper population fluctuations in Colorado. Environ. Entomol. 27, 892–901.

Caswell, H., John, A.M., 1992. From the individual to the population in demographic models. In: DeAngelis, D.L., Gross, L.J. (Eds.), Individual-based Models and Approaches in Ecology, Populations, Communities, and Ecosystems. Chapman & Hall, New York, pp. 36–66.

Chapman, R., Joern, A. (Eds.), 1990. Biology of Grasshoppers. Wiley, New York.

Church, N.S., Salt, R.W., 1952. Some effects of temperature on development and diapause in eggs of *Melanoplus bivittatus* (Say) (Orthoptera, Acrididae). Can. J. Zool. 30, 173–184.

Collett, M., Despland, E., Simpson, S.J., Krakauer, D.C., 1998. Spatial scales of desert locust gregarization. Proc. Natl. Acad. Sci. U.S.A. 95, 13052–13055.

Day, T., 2000. Competition and the effect of spatial resource heterogeneity on evolutionary diversification. Am. Nat. 155, 790–803.

Day, T., Rowe, L., 2002. Developmental thresholds and the evolution of reaction norms for age and size at life-history transitions. Am. Nat. 159, 338–350.

Dean, J.M., 1982. Control of diapause induction by a change in photoperiod in *Melanoplus sanguinipes*. J. Insect Physiol. 28, 1035–1040.

Duke, K.M., Crossley, D.A., 1975. Population energetics and ecology of the rock grasshopper, *Trimertropis saxatilis*. Ecology 56, 1106–1117.

Durrett, R., Levin, S., 1993. The importance of being discrete (and spatial). Theor. Popul. Biol. 46, 363–394.

Fielding, D.J., Brusven, M.A., 1990. Historical analysis of grasshopper (Orthoptera: Acrididae) population responses to climate in southern Idaho, 1950–1980. Environ. Entomol. 19, 1786–1791.

Fielding, D.J., Brusven, M.A., Shafii, B., Price, W.B., 2001. Spatial heterogeneity of low-density populations of *Melanoplus sanguinipes* in response to livestock grazing and vegetation treatments. Can. Entomol. 133, 843–855.

Flanagin, V.L., Haase, S.P., Juliano, S.A., 2000. Effects of growth rates on development to metamorphosis in the lubber grasshopper, *Romalea microptera*. Oecologia 125, 162–169.

Gangwere, S.K., Muralirangan, M.C., Muralirangan, M. (Eds.), 1997. The Bionomics of Grasshoppers, Katydids and Their Kin. Cab International Publ., London.

Grant, A., Hassall, M., Willott, S.J., 1993. An alternative theory of grasshopper life cycles. Oikos 66, 263–268.

Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future? Ecol. Model. 115, 129–148.

Grimm, V., Uchmanski, J., 2002. Individual variability and population regulation: a model of the significance of within-generation density dependence. Oecologia 131, 196–202.

Gyllenberg, G., 1974. A simulation model for testing the dynamics of a grasshopper population. Ecology 55, 645–650.

Haferkamp, M.R., Volesky, J.D., Borman, M.M., Heitschmidt, R.K., Currie, P.O., 1993. Effects of mechanical treatments and climatic factors on Northern Great Plains rangelands. J. Range Manage. 46, 346–350.

Hardman, J.M., Mukerji, M.K., 1982. A model simulating the population dynamics of the grasshoppers (Acrididae) *Melanoplus sanguinipes* (Fabr.), *M. packardii* Scudder, and *Camnula pellucida* (Scudder). Res. Popul. Ecol. 24, 276–301.

Higgins, L., 2000. The interaction of season length and development time alters size at maturity. Oecologia 122, 51–59.

Higgins, L.E., Rankin, M.A., 1996. Different pathways in arthropod postembryonic development. Evolution 50, 573–582.

Joern, A., Behmer, S.T., 1997. Importance of dietary nitrogen and carbohydrates to survival, growth, and reproduction in adults of the grasshopper *Ageneotettix deorum* (Orthoptera: Acrididae). Oecologia 112, 201–208.

Joern, A., Behmer, S.T., 1998. Impact of diet quality on demographic attributes in adult grasshoppers and the nitrogen limitation hypothesis. Ecol. Entomol. 23, 174–184.

Joern, A., Gaines, S.B., 1990. Population dynamics and regulation in grasshoppers. In: Chapman, R.F., Joern, A. (Eds.), Biology of Grasshoppers. Wiley, New York, pp. 415–482.

Joern, A., Klucas, G., 1993. Intra- and interspecific competition in adults of two abundant grasshoppers (Orthoptera: Acrididae) from a sandhills grassland. Environ. Entomol. 22, 352–361.

Kemp, W.P., Cigliano, M.M., 1994. Drought and rangeland grasshopper species diversity. Can. Entomol. 126, 1075–1092.

Klingenberg, C.P., Spence, J.R., 1997. On the role of body size for life-history evolution. Ecol. Entomol. 22, 55–68.

Knapp, A.K., Smith, M.D., 2001. Variation among biomes in temporal dynamics of aboveground primary production. Science 291, 481–484.

Mann, R., Pfadt, R.E., Jacobs, J.J., 1986. A simulation model of grasshopper population, dynamics and results for some alternative control strategies. University of Wyoming Agricultural Experiment Station Science Monograph, vol. 51. pp. 1–48.

McGinnis, A.J., Kasting, R., 1967. Dietary cellulose: effect on food consumption and growth of a grasshopper. Can. J. Zool. 45, 365–367.

Nylin, S., 2001. Life history perspectives on pest insects: what's the use? Aust. Ecol. 26, 507–517.

Nylin, S., Gotthard, K., Wiklund, C., 1996. Reaction norms for age and size at maturity in *Lasiommata* butterflies, predictions and tests. Evolution 50, 1351–1358.

Oedekoven, M.A., Joern, A., 2000. Plant quality and spider predation affects grasshoppers (Acrididae): food quality-dependent compensatory mortality. Ecology 81, 66–77.

O'Neill, K.M., Woods, S., Streett, D., O'Neill, R.P., 1993. Aggressive interactions and feeding success of scavenging grasshoppers (Orthoptera: Acrididae). Environ. Entomol. 22, 751–758.

Parker, J.R., 1930. Some effects of temperature and moisture upon *Melanoplus mexicanus mexicanus* Saussure and *Camnula pellucida* Scudder (Orthoptera). University of Montana Agricultural Experiment Station Bulletin, vol. 223. 132 pp.

Peitgen, H., Saupe, D., 1988. The Science of Fractal Images. Springer-Verlag, New York.

Pfadt, R.E., 1949. Food plants as factors in the ecology of the Lesser Migratory grasshopper *Melanoplus mexicanus* (Sauss.). University of Wyoming Agricultural Experiment Station Bulletin, vol. 290. pp. 1–51.

Pfadt, R.E., 1994. Field Guide to Common Western Grasshoppers, 2nd ed. Wyoming Agricultural Experiment Station Bulletin 912.

Pfadt, R.E., Smith, D.S., 1972. Net reproductive rate and capacity for increase of the migratory grasshopper, *Melanoplus sanguinipes* (F.). Acrida 1, 149–165.

Pickford, R., 1962. Development, survival and reproduction of *Melanoplus bilituratus* (Wlk.) (Orthoptera: Acrididae) reared on various food plants. Can. Entomol. 92, 1–10.

Railsback, S.F., 2001. Concepts from complex adaptive systems as a framework for individual-based modelling. Ecol. Model. 139, 47–62.

Rees, M., Sheppard, A., Briese, D., Mangel, M., 1999. Evolution of size-dependent flowering in *Onopordum illyricum*, a quantitative assessment of the role of stochastic selection pressures. Am. Nat. 154, 628–651.

Rodell, C.F., 1977. A grasshopper model for a grassland ecosystem. Ecology 58, 227–245.

Roff, D.A., 1992. The Evolution of Life Histories; Theory and Analysis. Chapman & Hall, New York.

Scheiner, S.M., 1998. The genetics of phenotypic plasticity: VII. Evolution in a spatially-structured environment. J. Evol. Biol. 11, 303–320.

Schmitz, O., 2000. Combining field experiments and individual-based modeling to identify the dynamically relevant organizational scale in a field system. Oikos 89, 471–484.

Schmitz, O., Booth, G., 1997. Modelling food web complexity: the consequences of individual-based, spatially explicit behavioural ecology on trophic interactions. Evol. Ecol. 11, 379–398.

Sibly, R.M., Monk, K., 1987. A theory of grasshopper life cycles. Oikos 48, 186–194.

Simpson, S.J., Abisgold, J.D., 1985. Compensation by locusts for changes in dietary nutrients: behavioural mechanisms. Physiol. Entomol. 10, 443–452.

Smith, D.S., 1968. Oviposition and fertility and their relation to copulation in *Melanoplus sanguinipes* (F.). Bull. Entomol. Res. 57, 559–565.

Stearns, S.C., Koella, J.C., 1986. The evolution of phenotypic plasticity in life-history traits. Predictions of reaction norms for age and size at maturity. Evolution 40, 893–913.

Strand, E., Huse, G., Giske, J., 2002. Artificial evolution of life history and behavior. Am. Nat. 159, 624–644.

Tatar, M., Gray, D.W., Carey, J.R., 1997. Altitudinal variation for senescence in *Melanoplus* grasshoppers. Oecologia 111, 357–364.

Tenhumberg, B., Tyre, A.J., Roitberg, B., 2000. Stochastic variation in food availability influences weight and age at maturity. J. Theor. Biol. 202, 257–272.

Thompson, D.B., 1999. Genotype-environment interaction and the ontogeny of diet-induced phenotypic plasticity in size and shape of *Melanoplus femurrubrum* (Orthoptera: Acridiae). J. Evol. Biol. 12, 38–48.

Thorhallsdottir, T.E., 1990. The dynamics of a grassland community: a simultaneous investigation of spatial and temporal heterogeneity at various scales. J. Ecol. 78, 884–908.

Uchmanski, J., 2000. Individual variability and population regulation: an individual-based model. Oikos 90, 539–548.

Uchmanski, J., Grimm, V., 1996. Individual-based modelling in ecology: what makes the difference? Trends Ecol. Evol. 11, 437–441.

Wall, R., Begon, M., 1986. Population density, phenotype, and mortality in the grasshopper *Chorthippus brunneus*. Ecol. Entomol. 11, 445–456.

Warren, J., Topping, C., 2001. Trait evolution in an individual-based model of herbaceous vegetation. Evol. Ecol. 15, 15–35.

Wilson, W.G., 1998. Resolving discrepancies between deterministic population models and individual-based simulations. Am. Nat. 151, 116–134.

Yang, Y., Joern, A., 1994a. Compensatory feeding in response to variable food quality by *Melanoplus differentialis*. Physiol. Entomol. 19, 75–82.

Yang, Y., Joern, A., 1994b. Gut size changes in relation to variable food quality and body size in grasshoppers. Funct. Ecol. 8, 36–45.